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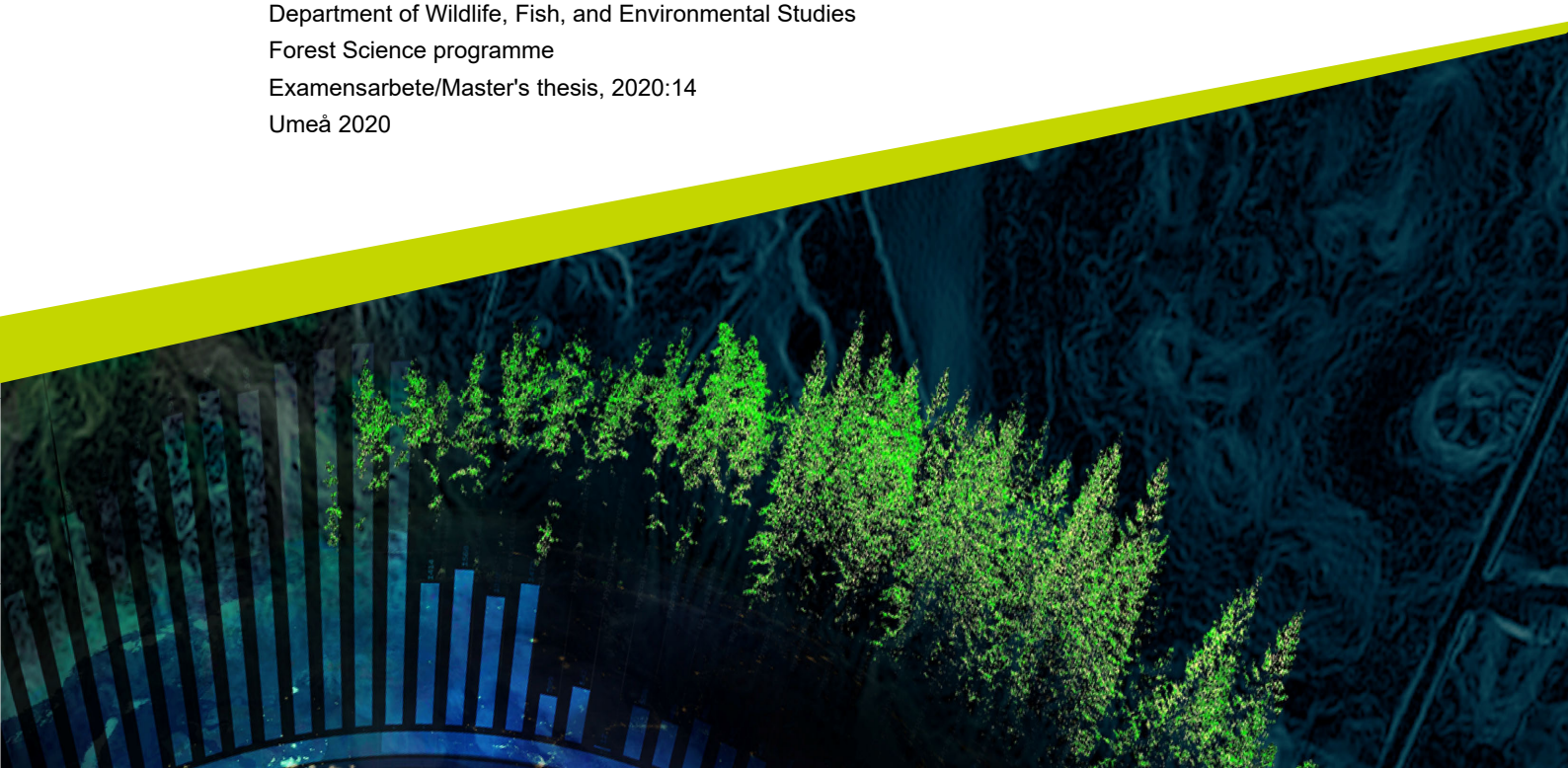

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Abstract

Intraspecific differences in movement over time occur across many taxa. In moose (*alces alces*), such behaviour has been seen during the rut. Knowledge about behavioural patterns can improve management since it can act as a tool in decision-making. Sweden's moose population has a skewed sex ratio to the benefit of females as a result of the current hunting system. Skewed sex ratio can have negative impact on populations since it can cause breeding with individuals that otherwise would not have been selected for. Therefore, I tested for differences between male and female moose in movement speed and the impacts of age and the time of day. I also tested the size of the home range and the intrasexual differences in male movement speed depending on observed proportion of male moose. The data came from GPS-marked adult moose in Sweden. The study areas reached from Norrbotten county in northern Sweden to Kronoberg county in the south. Due to geographical and climatic differences across Sweden, I divided the study into a northern and southern area. I used a linear mixed model for the analyses, except when testing the movement speed across the day. Here I used a generalized additive mixed model to account for non-linear movement. I analysed data of 622 individuals (females=464, males=184). Male movement speed was always higher than for females, except for moose above the age of 13 in northern Sweden. The movement speed over the day showed a bimodal distribution for both northern and southern areas, with the peaks matching timing of dawn and dusk. The pattern of the changes in movement speed shared high similarities between sexes, but females had a constantly lower movement speed than the males. Predicted movement speed of males in southern Sweden compared to the observed proportion of male moose, to my surprise, showed a decrease with increasing male proportion. In northern Sweden, I found no relationship between male moose movement and proportion of males in the area. Home ranges were at both 50 and 95% estimate larger for male moose than for female moose in both northern and southern areas. The higher movement rate and home ranges of male moose could reduce the effect of negative impacts of a skewed sex ratio. Prime aged male moose move more than not primed age males and for that reason may increase their chances to breed with several females. Future studies of rutting behaviour may benefit from comparing the differences between rutting season and other season to unravel what in these intraspecific differences that is induced by the rut.

Keywords: movement speed, home range, age, dawn, dusk, sex ratio, Alces alces

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1 Introduction

Across many animal taxa, variation in movement can be seen between seasons (Zeng et al. 2010; Lapointe et al. 2013; Ruiz-Gutierrez et al. 2016), and these variations can also occur over shorter (such as day and night) and longer (such as winter and summer) temporal scales as well as on smaller and larger spatial scales (Leblond et al. 2010). Such variations are known to occur in ungulates (van Beest et al. 2013; Ofstad 2013), and among moose (Alces alces) variation occurs within the species at both the temporal and spatial scale (Bunnefeld et al. 2011; Leblond et al. 2010; Cederlund & Sand 1994).

Intraspecific difference in the movement behaviour of moose has been seen during the rut. In Canada, male moose kept a higher movement rate than females during the rut (Leblond et al. 2010), and Alaskan bull moose did not eat for two weeks during the rut (Miguelle 1990). Previous studies also suggest that female moose move less than the males during the rut (Neumann & Ericsson 2018) and have a smaller home range than the males (Cederlund & Sand 1994)

In moose, the home range size is strongly affected by the access to forage (van Beest et al. 2010). This would naturally lead to a denser population where carrying capacity is high, however, this natural distribution of the moose population can be strongly affected by anthropogenic interference such as fragmentation of the landscape (Borowik et al. 2020), and hunting. Other factors that affect the density of a population could be presence of carnivores (Gallagher et al. 2017), and diseases as e.g. natural causes.

The most direct way that humans can affect the moose population is through harvest (Fenberg & Roy 2008), and the Swedish moose population is heavily managed. Sweden´s population of moose has increased from approximately 90 000 individuals in 1955 to 230 000 individuals in 2005 (Bergström & Danell 2009), and the annual harvest is around 30 % of the

total population (Svenska Jägareförbundet). In Sweden, the moose population is being carefully managed through the annual harvest were the quota are pre-set in relation to different management goals, e.g. to decrease damage to forestry (Öhman et al. 2011) as well as reduce number of car accidents (Neumann et al. 2011).

Moose are managed within moose management areas (Älgförvaltingsområde, MMA) and each management area includes several hunting parishes (Älgskötselområde) (SFS 1987:905). Management areas vary in size across latitudes (www.lansstyrelsen.se), the larger areas are found on higher latitudes, aiming to catch variation in movement strategies among popu-lations (Allen 2016). Management goals are set for three years at the time and must be approved by the corresponding County Administrative Board (www.lansstyrelsen.se).Within the management areas, landowners and hunters jointly decide on offtake based on the status of the population and local management goals (SFS 1987:905). The hunt is then carried out by local hunters that are expected to implement the decision on the harvest rates.

Since the individual hunter is the one making the decision whether to shoot a moose or not this can have additional impact on the population if certain traits (such as big antlers) are selected for. Size selective harvest can affect many traits in a population such as demography, life history, genetics and behaviour (Fenberg & Roy 2008), and intense harvest of a specific gender will create a skewed sex-ratio (Milner et al. 2007). A higher harvest of males reduces the percentage of adult male moose, which can cause females to breed with younger males that have not yet reached their prime age. In areas with fewer males, the existing males have a decreased growth, resulting in smaller males (Garel et al. 2006). When the females breed with smaller/ pre prime age males, the birthweight of calves can be reduced (Milner et al. 2007). Reduced birthweight can also be caused by senescence in females (Ericsson et al. 2001). The birthweight is used as an indicator of the populations condition (Danell et al. 2011). In addition, the Swedish harvest system benefits females giving birth to several calves, since the calves work as a life insurance for the females (Ericsson et al. 2001; Nilsen & Solberg 2006), because the hunters have to shoot the calf before the female. As a result, female moose have a higher survival than the males (Solberg et al. 2000).

Knowledge of moose movement during the rut could allow for a more selective harvest and thereby reduce unwanted effects on the population e.g. skewed age distribution and sex ratio and effects thereof if it is possible

while at the same time pursuit other existing management goals. The aim of the thesis is to study intraspecific differences in moose during the rut since increased knowledge can help future management decisions. I would like to see how movement differs between male and female moose, and also see if the sex ratio have an affect on male moose. Based on this I formulated four hypothesis. Knowledge of moose movement during the rut could allow for a more se-lective harvest and thereby reduce unwanted effects on the population, e.g. skewed age distribution and sex ratio and effects thereof if it is possible while at the same time pursuit other existing management goals. The aim of the thesis is to study intraspecific differences in moose during the rut since increased knowledge can help future management decisions. I would like to see how movement differs between male and female moose, and also if the sex ratio has an effect on male moose. Based on this I formulated four hypothesis.

Previous research have seen higher movement speed in males (Neumann & Ericsson 2018), and increased participation in rutting of males with in-creasing age (Mysterud et al. 2005; Miquelle 1990), therefore I expect a higher movement speed of older males during the rut than for females (1th hypothesis), since males seem to be more prone to search for a mate than the females. This also connect to the second hypothesis, that the male will have a larger home range whilst females will be expected to have a smaller home range (2nd hypothesis) during the rut.

For both genders, I expect the movement speed to be largest during dawn and dusk (3rd hypothesis) as has been seen in previous movement anal-yses of moose in Sweden (Neumann & Ericsson 2018).

I also expect the males to have equal movement speed independent of varying sex ratio (4th hypothesis), based on the findings of Mysterud et al. (2005) that did not find a correlation between reproductive effort and sex ratio.

2 Method

For this study, I analysed pre-collected spatial position data from GPS-marked adult moose (females= 464, males=158) in Sweden. The data were from moose in southern and northern areas across 12 degrees of latitude (ca 1350km). The study sites were in Norrbotten (BD) and Västerbotten (AC) county in northern Sweden. In the south, data was collected in the county of Södermanland(D) and Kronoberg(G)/Kalmar(H)(*Figure1*). The earliest data were collected in 2003 in Norrbotten, and in 2005, data collection started in Västerbotten and the southern areas contain data from 2009. The last year of data collected used in this study was 2018.

I analysed moose position data between 1 September and 31 October each year to cover the rutting season based on Neumann & Ericsson (2018). The data was gathered within several different projects and collected with GPS/GSM-collars. To be able to use the observation from each year independently from each other, I assigned individual moose-year IDs. I subset the data so that I only used observations collected within five minutes from the full hour.

The data was then analysed with R version ”3.6.2” using the package, adehabitatHR, maptools, dplyr, plyr, ggplot2, nlme, ggeffects, mgcv, sp and suncalc. To be able to study the movement of moose during the rutting season, I used the observations taken

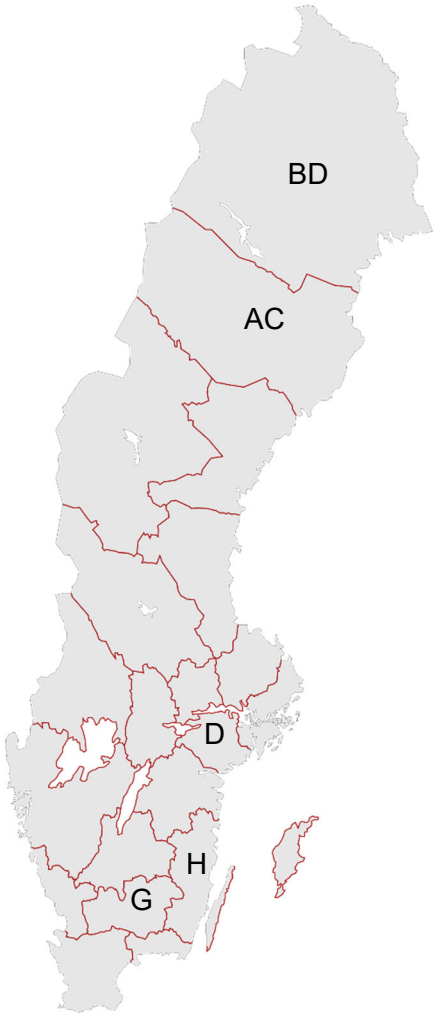

Figure 1: Map with the areas used in this study marked out. BD=Norrbotten, AC=Västerbotten, D=Södermanland, G=Kronoberg & H=Kalmar. CC BY-SA

during the full hour (1-3 hours inter-vals). I calculated moose movement speed as the Euclidian distance be-tween two spatial points gathered successional and then divided that dis-tance by the time elapsed giving the speed as m/hr.

Positions were visually assessed for spatial outliers. Outliers were removed since they were considered as sampling errors. Since the study focuses on moose that are affected by rutting, I focused on adult moose and removed a small group of females at age 1 since they are not considered to participate in rutting activity. Sand & Cederlund (1996) showed that only 1,3% of the two-year olds had been pregnant, which was confirmed by Ericsson et al. (2001) that saw no offspring in two-year olds.

I assigned each gender to an area (hereafter referred to as north or south) resulting in four groups (Females north, Females south, Males north and Males south). North cover data from Norrbotten and Västerbotten while south includes data from Södermanland, Kronoberg and Kalmar (*Figure1*). The main reason for this being that previous studies show that rutting occurs at different times in northern and southern Sweden. Saether et al. (1996) saw a latitudinal delay on ovulating time in moose in Norway. Neumann et al. (2020) showed that calving occurs ca 2-3 weeks later for females in northern Sweden than in southern Sweden, which means that also the rutting time differs.

To meet the assumption on normality in the data, I log transformed my response variables (*Table 1*). After running the models for each of the hypotheses, I used the model outputs to make predictions of the expected values at different values of the explanatory variable (package ggeffects). Some individuals were lacking a year of birth, those individuals could not be used when analysing the age and therefore those individuals were removed since I wanted to be certain that I only used data from individuals 2 years or older.

To test for the effect of age on movement speed (hypothesis 1), I calculated moose age each given year based on its estimated year of birth, as determined by tooth wear during marking procedure (Ericsson and Wallin 2001). I applied a linear mixed model (package nlme) to test for gender differences (*Table 1*), because I had repeated measures as the same moose could appear several years in the study, which I needed to account for when studying age groups.

To create a spatial grid, I used the spatial information connected to each observation and connected those to the IDs and the time data. From that spatial grid, I could then calculate the bursts between two observations. These bursts are an estimate of the moose movement between two following occasions in a trajectory layer. I created a spatial grid for each individual moose-year ID based on the spatial distribution of its position data. For each moose-year ID, I estimated the home range on a given spatial grid using the biased random bridge function (BRB, package adehabitatHR) to answer my second hypothesis. This function is an extension of the Brownian Bridge Movement Model that considers the time elapsed between following positions and the autocorrelation inherent in GPS data. The BRB function considers animal movement, activity, and boundaries when estimating home range sizes (Benhamou & Cornélis, 2010). I set the longest time between two relocations to 2 days and the shortest distance to 0. The extent of the grid was set to 0.1. Due to the large data amount and computational restrictions, I subsampled my original data set to four positions per day and moose as was done by Allen et al. 2016, selecting positions at 06:00, 12:00, 18:00 and 00:00. The error of the moose movement (sig2) were set to 20 meters and the parameter for the variance in motion (sig1) was calculated for each animal individually (Calenge, 2015). Using a linear mixed model (package nlme), I then analysed the home range estimates for 95 and 50 percentage usage (package adehabitatHR, maptools). (*Table 1*)

For the third hypothesis, I used a generalized additive mixed model to meet the non-linearity in moose movement over day, since previous studies have shown a bimodal distribution of moose activity patterns over the day (Neumann et.al 2012). Due to the data size, a subset was needed to run the generalized additive mixed model (package mgvc) (*Table1*). Data was subset to 25 % using random sampling without replacement. The time (hour of the day) was specified to be cyclical smoothed. To estimate the time for dawn and dusk, I used suncalc package within R. Suncalc allowed me to calculate the dawn and dusk for each GPS -coordinate at the day of the collection of that datapoint. From these calculations, I could then estimate the mean time for dawn and dusk and the standard deviation in each area.

For hypothesis four, I collected additional data on the proportion of male moose from Viltdata (Svenska Jägareförbundet), where yearly observations and numbers of shot moose are reported and published from the first week of the annual moose hunt. I chose to use the proportion of males amongst adult moose rather than the amount of shot moose. The reason for this is that observations are less likely to be biased than the numbers of harvested animals, where a calf works like a life insurance for the females. Hunters must shoot the calf before they shoot the female (SFS 1987:905). The time delay before a shot can be taken at the female usually result in her managing to escape, and Ericsson and Wallin (2001) state that male moose runs a higher risk of dying than females. To answer the fourth hypothesis, I only analysed data of male moose. I connected each moose position to a moose management area (MMA) and assigned the proportion of males observed to that area and the year of the observation. As for the first and second hypothesis, I used a linear mixed model (package nlme). Data was subset to 25 % to be able to run the model. (*Table 1*).

Table 1. The different models used for each hypothesis and the model inputs. Model lme represent a linear mixed model and gamm a generalized additive mixed model.

Hypothesis	Response variable	Explanatory variable	Random factor	Model	Subset	Data
1	Logarithmic movement speed	Sex * Age	Moose ID	lme	-	
2	Home range	Sex	Moose ID	lme	4 obs/day	95% and 50% estimates
3	Logarithmic movement speed	Sex * Hour	Moose ID	gamm	25%	
4	Logarithmic movement speed	Observed proportion of males	Moose ID	lme	25%	

3 Results

3.1 The shape of the data

I analysed data from 622 individuals in this study. Of those 434 were found in northern Sweden and 188 in southern Sweden, resulting 1629 (north n= 1058, south n=571) unique moose-year IDs. The females were represented in 1299 of those IDs while males stood for 330.

In northern Sweden, the observed moose mean age was lower than in southern Sweden, but the standard deviation was large for all groups (*Table 2*). Females were on average older than males in both regions (*Table2*) The oldest females observed in the northern (*Figure 2*) and southern (*Figure 3*) area were both 18 years while the oldest male in the north were 17 and in the south 13. The observations of male moose that belong to age group 15, 16 and 17 in northern Sweden are based on the same moose. This could be the result, since I gave every moose a unique moose-year ID.

Table 2. Mean age and the standard deviation for the four different groups "Female north", "Male north", "Female south" and "Male south"

Group	Female North	Male North	Female South	Males South
Mean age	7.2	5.3	8.9	6.1
Standard deviation	2.9	2.3	3.7	2.5

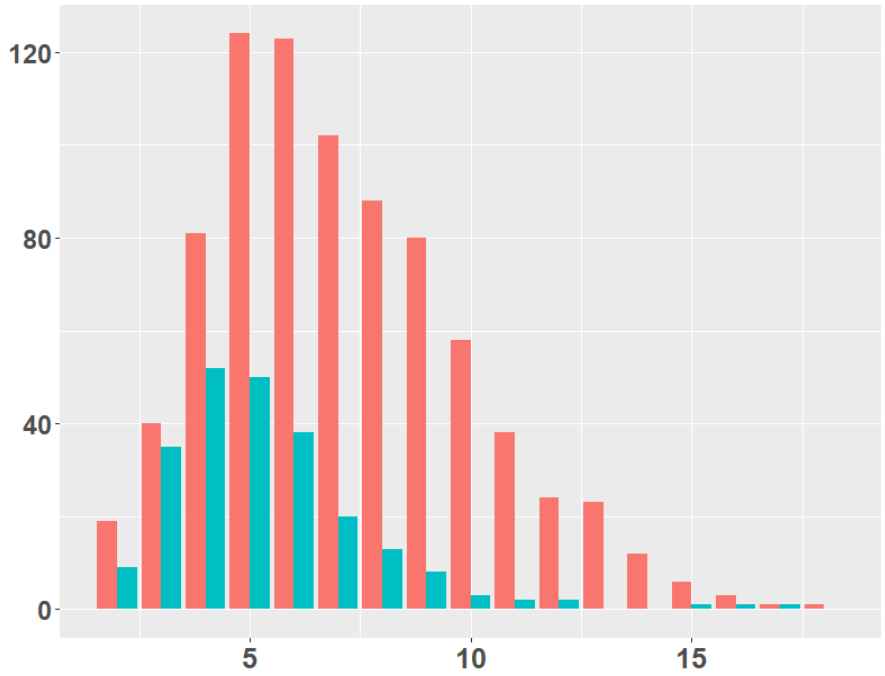

Figure 2. Age distribution in northern Sweden. The Y-axis shows the number of animals and the X-axis shows the age starting from 2 years. Blue is males and pink is females.

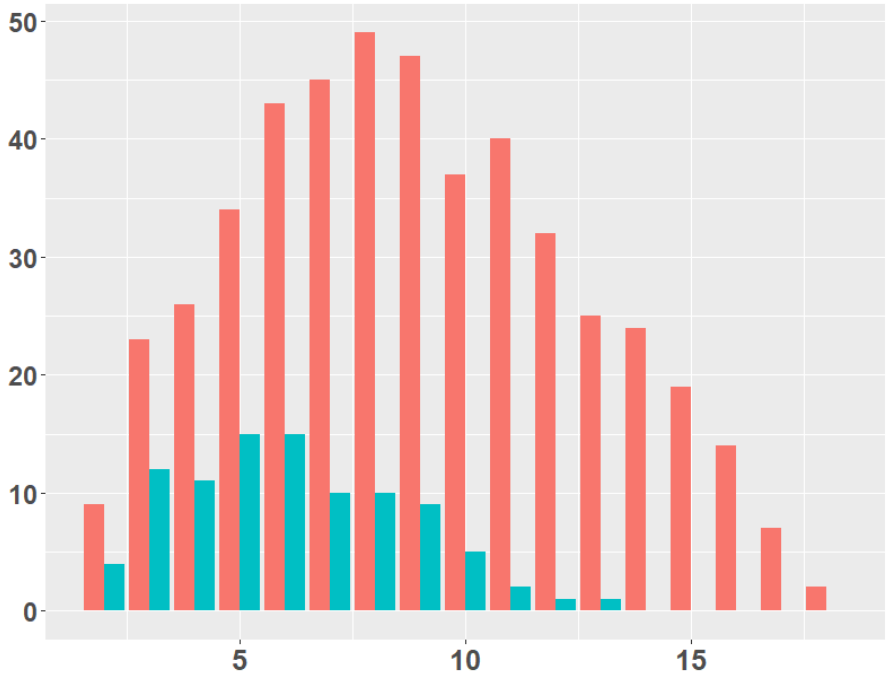

Figure 3. Age distribution in southern Sweden. The Y-axis shows the number of animals and the X-axis shows the age starting from 2 years. Blue is males and pink is females.

3.2 Hypothesis 1

3.2.1 Northern Sweden

Males in northern Sweden moved less with increasing age compared to female moose ($t(1,1076913)=9.2$, $p<0.0001$). Females also showed a decrease in movement with increasing age, but the decrease was smaller than for males. The predicted male movement was higher than the female movement until they are circa 13 years (Figure 4).

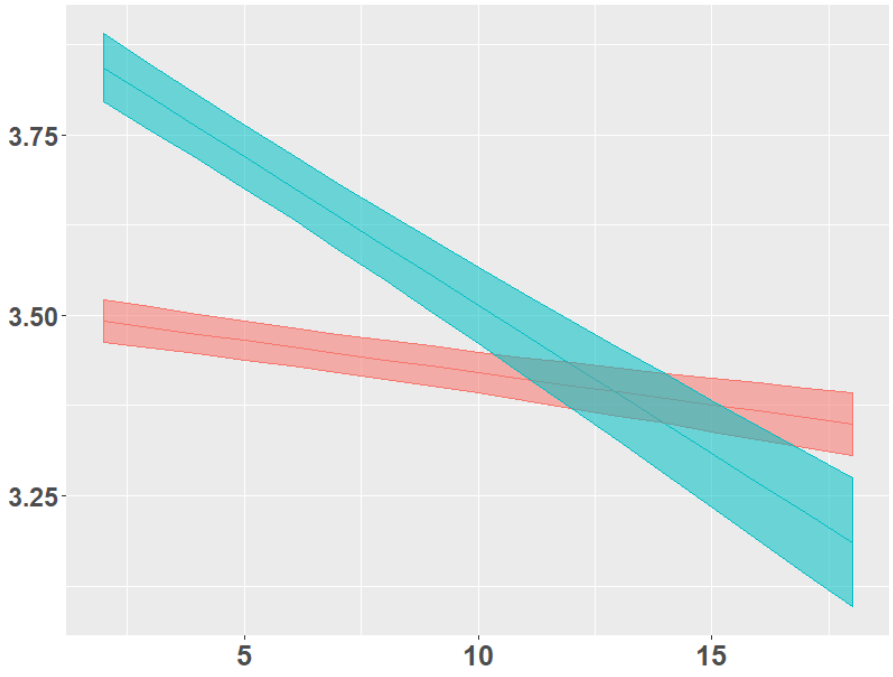

Figure 4. The predicted line ± 95 % confidence intervals of moose movement activity (m/hr, y-axis) in relation to age in northern Sweden as given by the linear mixed model. Values of movement activity are log-transformed. Blue represent male and pink female movement.

3.2.2 Southern Sweden

In southern Sweden, males moved less with increasing age compared to female moose (t(1, 495226)=2.4, p=0.019). Males had a higher movement speed than females across all ages (males: t(1,424)=4.6, p<0.0001). The prediction showed a decrease in movement with increasing age (*Figure 5*).

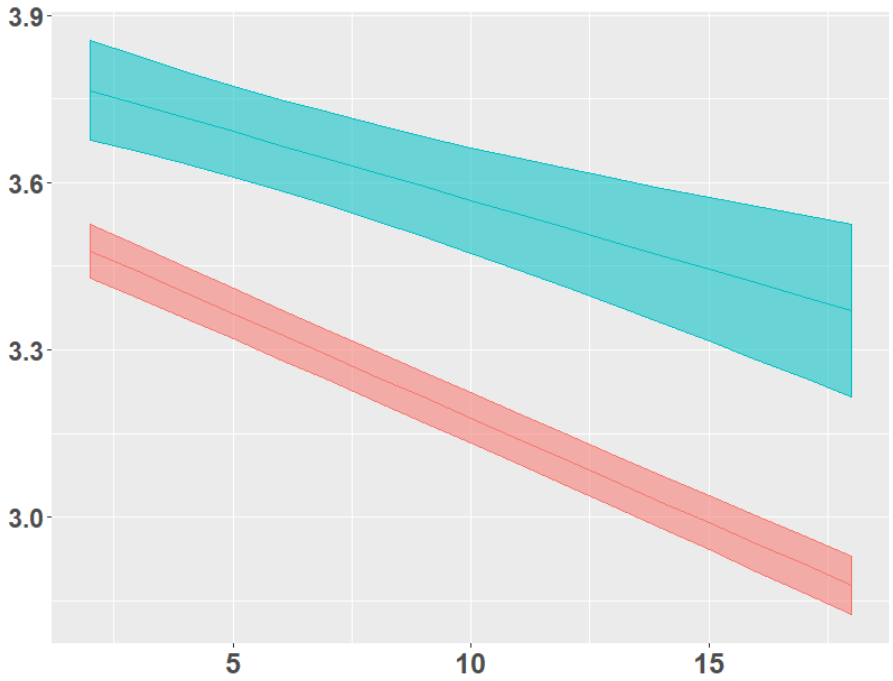

Figure 5. The predicted line ± 95 % confidence intervals of moose movement activity (m/hr, y-axis) in relation to age in southern Sweden as given by the linear mixed model. Values of movement activity are log-transformed. Blue represent male and pink female movement.

3.3 Hypothesis 2

In both northern and southern Sweden, male moose had larger home ranges than females when estimating both the 95% kernel and the 50% kernel. Males in northern Sweden also had a larger home range than males in southern Sweden and females in northern Sweden had a larger home range than females south. (*Table 3 and table 4*)

Table 3. The different predicted home range sizes log-transformed for male and female moose in northern and southern Sweden at a 95 and 50 percentage estimate.

Region	Estimate	Female	Male	Stats
N	95	7.32± 0.07	8.16 ±0.12	t(1,563)=218.62, p<0.0001
N	50	5.62±0.06	6.4±0.12	t(1,563)=175.6, p<0.0001
S	95	6.44± 0.06	7.61±0.12	t(1,289)=214.49, p<0.0001
S	50	4.93±0.06	6.06±0.12	t(1,289)=162.29, p<0.0001

Table 4. The different predicted home range sizes in hectare for male and female moose in northern and southern Sweden at a 95 and 50 percentage estimate.

Region	Estimate	Female	Male
N	95	1510	3498
N	50	276	602
S	95	626	1998
S	50	138	428

3.4 Hypothesis 3

3.4.1 Northern Sweden

I found two visible peaks in movement speed during the day for both female and male moose in northern Sweden with the largest at 15:00, the second largest ca 04:00 (female*time: t(1,267245)=251.59, p= p<0.0001; male*time: t(1,420)=10.59, p= p<0.0001). Movement speed in northern Sweden by the hour of the day were higher for males then females at a constant level over the day. The lowest levels of movement occur around midnight and 08:00 for both male and female moose (Figure 6).

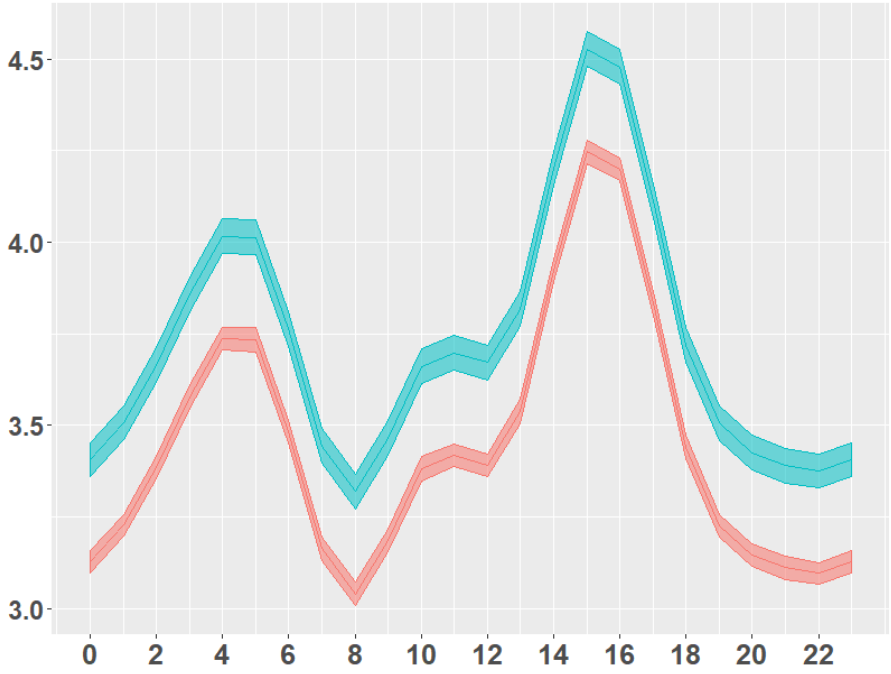

Figure 6. The predicted line+/-95% confidence intervals of moose speed (m/hr, y-axis) in relation to time of the day in northern Sweden as given by the generalized additive mixed model. Values of movement activity are log-transformed. Blue represent male and pink female movement.

3.4.2 Southern Sweden

As for moose in northern Sweden, I found two peaks in movement and both sexes moved in the same patterns over the day (female*time: t(1,130020)=169.02, p<0.0001; male*time: t(1,186)=10.83, p<0.0001). For southern Sweden, the largest peak occurred around 16:00 and the second largest at circa 04:00. The lowest movement is seen at circa 08:00. Males moved at a higher speed than females (*Figure 7*). Mean time for dusk and dawn was similar for northern and southern Sweden, but with larger standard deviations in the north (*Table 5*).

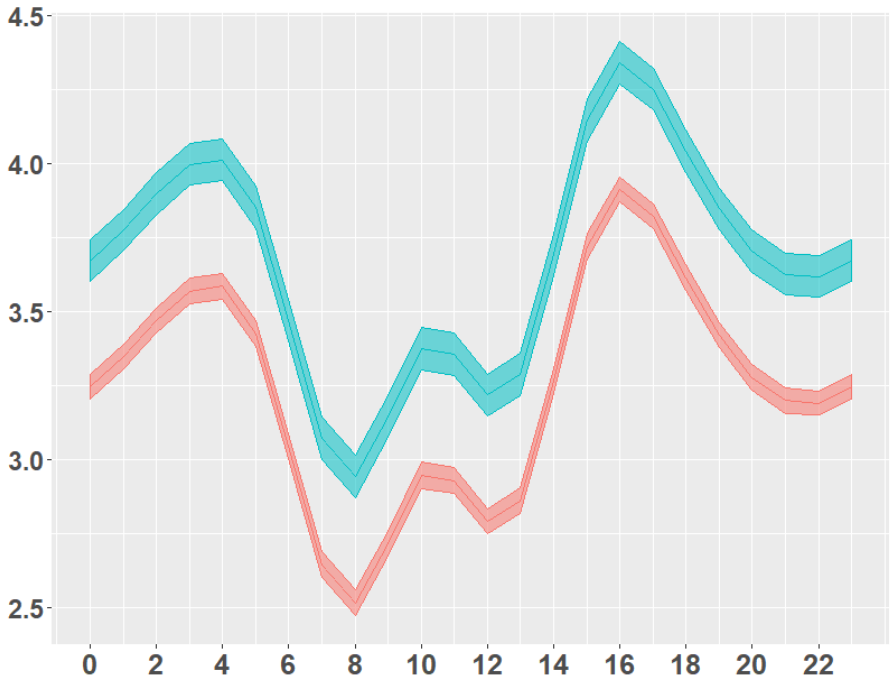

Figure 7. The predicted line+/-95% confidence intervals of moose speed (m/hr, y-axis) in relation to time of the day in southern Sweden as given by the generalized additive mixed model. Values of movement activity are log-transformed. Blue represent male and pink female movement.

Table 5. Mean time for dawn and dusk for the observations of this study with standard deviation for each area.

Area	Dawn	Dusk
North	03:56±1	17:19±1.1
South	04:16±0.37	17:21±0.47

3.5 Hypothesis 4

In southern Sweden, male moose showed a decrease in their movement with increasing proportion of males (t(1,22420)=-2.1, p=0.0379), for the northern males, the result was not significant (t(1,69983)=0.64, p=0.5211) (Figure 8).

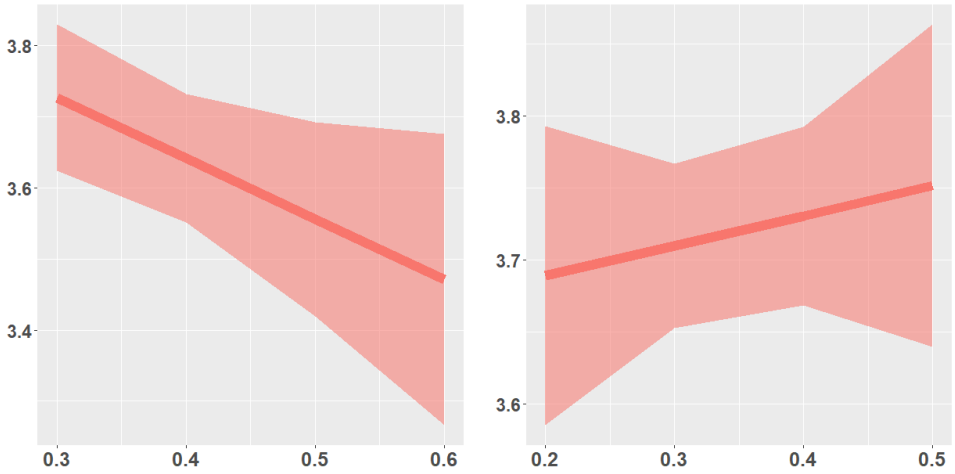

Figure 8. The predicted line ± 95 % confidence intervals of moose movement activity (m/hr, y-axis) in relation to observational data on the proportion of males in Sweden as given by the linear mixed model. Values of movement activity are log-transformed. The graph to the left represents southern male moose and the graph to the right represent northern male moose.

4 Discussion

Increased knowledge of moose behaviour can help to improve management of the species. Understanding how moose move and what is controlling that movement during the rutting season could help managers in the decision of how to set the harvest quota. For that reason, I have studied the movement during the rut of adult moose. I divided the study into a northern and a southern area to catch geographical differences in moose movement behaviour.

In both areas, my result suggest that male moose moved more than female moose. This is shown in higher movement speed and larger home range. The bimodal distribution of movement speed across the day has a similar appearance for northern and southern Sweden. Movement speed of male moose in southern Sweden showed a negative relationship to increasing proportion of males.

Older moose males move more during the rut than females (1th hypothesis)

I tested for differences in movement speed between male and female moose for different ages. My results suggest that males had a higher predicted movement speed than females in both northern and southern Sweden supporting my first hypothesis. Interestingly, I found a change in that relationship for northern Sweden at an age of 13 where the predicted movement speed of males become lower than that of the females.

My data set included a lot fewer position data of male moose than those for female moose. Within both areas, most data of male moose fell into younger age classes (97% of the male moose ≤ 10 yrs.). The heavily skewed distribution across ages in the male moose data may explain the small impact of older males on male movement in relation to female

moose. This could explain why the predicted line of males in northern Sweden cut the predicted line of the females. In southern Sweden, the predicted line of male moose suggests that males keep a higher movement speed than females independent of age. The result supported my first hypothesis that males move more than females in southern Sweden, but not in northern Sweden, which is likely due to the small sample size at high ages in this region. To be able to give a different result the number of males in the higher age group would need to be higher. Still the distribution of moose across the age groups is likely representative for the moose population. Few individuals of female moose reach the older age groups and even fewer males reach high ages.

As a part of my expectation that older males would move more than younger males and all females during the rut is the assumption that a prime aged male increase their movement. However, the definition of a prime age male differs among studies. Mysterud et al. (2005) suggest that males reach prime age around 6 years of age, whereas Malmsten et al. (2014) remove the focus from age to the condition of the male moose since body condition had a stronger effect on sperm quality then age itself. The condition of male moose declines after a certain age (e.g., after prime age) and this occurs around 12 years of age (Mysterud et al. 2005), suggesting that male moose above the age of 12 are not participating in the rutt in the same way as younger male moose do. Thus, the results of those past prime age moose might therefore not be relevant for my study. Since I used a linear model to answer the first hypothesis, I did not account for such a non-linear relationship. For a future study, it could be relevant to either remove males above a certain age, group males as either ”prime aged” or “not prime aged” or use a non-linear model that allows for non-linear variation across the ages to fully investigate the effect of age on the male movement during the rut.

Male moose range over a larger area during the rut than female moose (2nd hypothesis)

For my second hypothesis, I tested for differences in the size of female and male moose home range, using 95 and 50% home range estimates (Calenge 2015; Benhamou & Cornélis 2010). My results emphasize that male moose utilize a larger area during the rut than females as indicated by larger home ranges on both the 95% and 50% level, which confirms my second hypothesis. For this study, I only tested for differences between the sexes without considering moose age. Yet, additional variation could be expected across age groups. Cederlund & Sand (1994) saw an increase in

home range with increasing age for males while females home range were constant across ages. My results suggest that the moose population might stand a resilience against the human induced effects of a sex ratio that is skewed towards females, because the higher movement among males across larger areas may allow them to encounter more females than they would have at a lower level of movement and at a smaller home range. Even if the male moose got the ability to breed with several females, Malmsten et al. (2014) suggest that the males are not anatomically adapted for mating with several females. If so, the larger male home range might not have a direct impact on negative effects of a skewed sex ratio. A Canadian study saw no difference in reproduction in moose between harvested and unharvested areas (Laurian et al. 2000), while a study on moose sex ratio in Norway on the other hand saw an impact of lower proportion of males on the condition of next year's offspring (Sæther et al. 2003). In my study, all areas had low observed proportion of males (<40% observed males in 87,5% of the areas, always less than 50%), which could be affecting the home range to grew larger for the males. If that is the case, current management system might have high impact on the condition of the population. Additionally, the largest impacts on the population, if the harvest is at a sustainable level, is phenotype-based selective harvest (Coltman et al. 2003). If the remaining males are of lower condition as a result of prime aged males being selected in harvest, the increased home range might not benefit the male fitness. If male moose do not have the ability to breed with several female because of low sperm quality, then, the larger areas they need to move over to be able to breed might further aggravate the sperm quality.

Both male and female moose are most active during the rut at dawn and dusk (3rd hypothesis)

As I tested for the movement over the day, the seen bimodal distribution aligned with result from previous studies (Neumann et al. 2012; Neumann et al. 2019). For both areas, the peaks in movement fitted the mean time for dawn and dusk well, confirming my third hypothesis that the movement would be at its largest during those times. The decrease in predicted movement speed during the day were lower in southern Sweden than northern. The lower movement can be an effect of higher mid-day temperatures in southern Sweden compared to northern Sweden (www.smhi.se). Moose are heat sensitive and reduce their movement during warm days (van Beest et al 2012; Ericsson et al. 2015). The impact of this result on

the direct management of moose is low, however the impact on knowledge of such a bimodal pattern can be a tool to in the pursuit of minimising car accidents by increasing driver awareness. The predicted cost of annual car accidents caused by animal-vehicle collision is approximately 406 million USD in Sweden alone (Gren & Jägerbrand 2019). A moose that has a high movement speed is also more likely to be observed than a moose that stand still or has a lower movement rate. This may lead to a bias in the collection of yearly hunter observations since moose are not as likely to be observed during all times. A higher movement rate in male moose might cause additional bias since the males are more likely to be observed.

Male moose have an equal movement rate independent of sex ratio (4th hypothesis)

Contradicting my 4th hypothesis that the movement speed of males would be the same independent of observed proportion of males, southern males showed a decreasing movement with increasing proportion of males. The result for northern Sweden were not significant and did confirm my hypothesis that there would be no difference. According to the findings of Mysterud et al. (2005) there were a lack of correlation between reproductive effort and varying sex ratio, still they saw an increased aging effect on males in female biased populations. That study was based on the body mass before and after the rut of the male moose since male moose stop eating during the rut. My result opposes that result if movement speed is a relevant measure for the reproductive effort, at least for southern Sweden.

I used the observational data on the proportion of males assigned to each moose management area (MMA). Since the MMA:s are larger in the northern than in the southern Sweden (www.lansstyrelsen.se), it is reasonable to question the differences in the precision of the data. The proportion is determined as the number of observations per observational hour in each MMA. Within larger areas the variation can also be expected to be larger, however, the available data only gives one value per MMA. Therefor a more correct value of the moose observations could be expected in the southern MMA:s since the observations are connected to a smaller area. The northern management areas are considerable larger than the southern ones in order to account for the migrational patterns of the moose, which is likely to give a larger variation within the observations of each MMA. As a result, in northern Sweden, the observational data on the proportion of

males may miss the within-area variation of the male to female ratio across a given unit (MMA).

The observed number of moose per observational hour differs between the areas of my study. The highest observed numbers are in the Södermanland and Kronoberg while Norrbotten, Västerbotten and Kalmar has lower values (*Figure 1*) (Svenska Jägareförbundet). This suggest that the population is bigger in Södermanland and Kronoberg than in the other counties. Still this could explain the higher overall movement speed and home ranges in the northern areas simply by the lower proportion of moose. One reason for a population to be smaller in certain areas is that the carrying capacity of the land is lower which would be reasonable to assume whit shorter seasons and lower temperatures in the northern latitudes (www.smhi.se).

This study contained a smaller sample size for males than for females, especially in the higher age groups where male observations often did not occur. Moreover, GPS-collared moose might have a higher survival rate than non-collared ones and therefore the few older aged moose within this study might even be overrepresentative when it comes to the proportion of older moose. The small sample size of male moose at higher age classes reduces the predictive power of my results as movement of single individuals can become more influential on the overall results, still the total sample size is large for both sexes. In addition, I only tested for differences within the rutting season between male and female moose, area, and age, but to fully see the effect the rut has on the movement, a comparison of moose movement during the rut and outside the rut would be needed.

Previous studies on Canadian moose have shown that male movement rate peaked during the rut, while females did not show such a change in movement (Leblond et al. 2010). Neumann and Ericsson (2018) saw similar behaviour in Swedish moose. This difference in movement rate during the rut might be the outcome of the benefits on fitness for a male moose that breeds with several females. No such benefits occur for the female moose, she can only breed with one male each year and therefore does not benefit from continued search after a mate once she has breed. Despite the increase in male moose movement, large Alaskan male moose were seen standing inattentive during large amount of times during the rut (Miquelle 1990). This time, outside the rutting season, could be expected used for foraging for these larger males. Smaller males also reduced feeding, but not to the same extent (Miquelle 1990). Younger males that have not reached a body mass that is required to produce high quality sperm

might still be affected by the hormones driving the rut, but instead prioritise foraging to increase advantages in future rutting seasons. Mysterud et al. (2005) saw that the reproductive effort increased with age, suggesting that younger males did not participate during rutting to the same extent as older males. They also saw that high density in males decreased the reproductive effort for male moose. My data result shows the highest expected movement speed in the lowest age groups. To test if the movement speed is connected to the reproductive effort in males, movement data needs to be combined with data on weight loss, since the weight loss seems to be a relevant measure on what the male moose does when not moving, e.g. participating in reproduction or investing in future reproduction (Mysterud et al. 2005; Miquelle 1990).

In my study, I been making a comparison between northern and southern Sweden over several years, but I have not considered other factors influencing moose behaviour over time. Resent and future years have and is likely to hold differences in as well climatic changes, composition of species and anthropogenic interferences at both a spatial and temporal scale. Differences seen in my study can change between the areas and might increase or decrease in the future. I have not focused on the effects of any of these factors on the movement speed and home range of moose during the rut, but it could for instance be reasonable to question impacts of increasing carnivore populations on the size of the home range as well as the movement speed (Gallagher et al. 2017). Looking at the presence of bears (*Ursus arctos*) in Sweden, very few have been seen in the southern areas of my study (www.naturvardsverket.se), but in the north, they are common. On the other hand, the presence of wolves (Canis lupus) are more common in southern Sweden but there are several observations in the north as well (Naturvårdsverket), those observations are likely to be wolves that came from Finland. Apart from carnivores, the ungulate populations differ between my study areas, based on the numbers of shot and road killed animals the northern areas have only a low presence of roe deer (*Capreolus capreolus*). Presence of red deer (*Cervus elaphus*) are uncertain and fallow deer (*Dama dama*) does not occur at all, while in the south all three ungulate species occur alongside with moose (Jarnemo et al. 2018). The presence of humans is also higher in the south than then the north (www.scb.se). A warmer climate is likely to decrease the movement speed in moose (Ericsson et al. 2015), no matter if it is the rutting season or not. Increase and/or introduction of other ungulates might also impact moose movement patterns. In retro perspective, it would have been interesting to compare the results from one year to another in this study to see

if there is a big between year variation. Such a result could then have been compared to other changes that might have had an impact, such as temperatures and variations in presence of other animals to see if there was an effect on the between year variation during the rut.

In summary, my results suggest a higher movement and larger home ranges in male moose compared to females across ages and independent of time of the day. In southern Sweden, the results showed that the proportion of males had an impact on the male movement speed. If increased movement has an impact on the condition of the male and therefore on the quality of the sperm this could mean that a more even sex ratio has benefits on the reproduction in the moose population. Solberg et al. (2002) saw an impact of the biased sex ratio on the fecundity of moose with both older first-time pregnancies in female moose as well as breeding later in the season thereby reducing survival chances for the calves. My results suggest that males in the south are affected in their behaviour by the low proportion of males and future management should focus on balancing the sex ratio to a level were the impact of skewed sex ratio cannot be seen on male movement thereby increasing the chances of a viable moose population.

For all my hypotheses, future comparison of moose movement behaviour between the rutting season and outside the rutting season would be relevant to see what the actual effect of the rut is. Senescence in moose start appearing approximately at 12 years of age (Ericsson et al. 2001; Mysterud et al. 2005). The impact of senescence on rutting behaviour is not clear and for future studies, it could be relevant to test for such differences. Data needed to test for such differences are already existing within the data collection of other studies and only needs to undergo analysis.

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